Behavioral responses to variable predation risk in the California spiny lobster *Panulirus interruptus*

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ABSTRACT: Shelter dwelling and gregariousness are behavioral strategies used by benthic marine organisms to reduce the risk of predator-induced mortality. For spiny lobsters, the relative and synergistic success of shelter dwelling and aggregation in reducing mortality may vary with the perceived risk of predation as well as the availability and size distribution of conspecifics and shelters. We tested how these factors influence antipredator behavior in the California spiny lobster *Panulirus interruptus* in southern California kelp forests. We measured shelter and lobster characteristics, predator density, relative lobster mortality outside of shelter, and quantified lobster antipredator behaviors in (1) the La Jolla Ecological Reserve (LJER), a marine protected area with high densities of large fishes known to be lobster predators, and (2) the Point Loma kelp forest, a nearby, heavily fished area. Predator densities and the relative mortality of tethered juvenile and adult lobsters were much higher in the LJER than in Point Loma, as was mean lobster size. In response to higher predation risk, solitary lobsters in the LJER used shelters more closely scaled to their body size than lobsters in Point Loma, thereby restricting predator access to shelters. In addition, aggregations of 2 or more lobsters were more frequent than expected by chance in the LJER, but not in Point Loma. Lobsters in Point Loma commonly were found outside of shelter during the day, whereas no lobsters ever were observed outside of shelter during daylight hours in the LJER. Overall, our results indicate that California spiny lobsters modify their antipredatory behaviors with level of predation risk and that behaviors designed to minimize predator-induced mortality are similar between California spiny lobsters and other spiny lobster species.

KEY WORDS: Spiny lobster · Predation · Shelter · Behavior · *Panulirus interruptus* · Tethering

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INTRODUCTION

In many marine systems, predation directly and indirectly influences community structure (Paine 1974), prey and predator population dynamics (MacLulich 1937, Estes et al. 1998, Vucetich et al. 2005), and the behavior of prey and predatory organisms (Holbrook & Schmitt 1988, Micheli 1997). For prey organisms, there are a variety of behavioral strategies that may reduce the risk of predator-induced mortality. Seeking shelter within or among structural elements of habitats, such as vegetation, dens, or crevices is one of the most common ways that prey species reduce mortality due to

predation (e.g. Stein 1977, Garcia & Sih 2003, Forrester & Steele 2004). Many organisms form social groups (e.g. fish schools) in which cooperation among individuals can reduce the per capita risk of predation (Seghers 1974, Cote & Jelnikar 1999, Kie 1999). Grouped prey may more efficiently detect predators and may more effectively ward off predators than solitary prey. Additionally, for prey organisms that aggregate in structured habitats to avoid predators, gregarious behavior may guide prey more quickly to refuge (Childress & Herrnkind 1997).

For a given risk of predation, the relative and synergistic success of shelter dwelling and aggregation in

reducing prey mortality will vary with availability and size distribution of conspecifics and the availability and size-distribution of shelters (Eggleston et al. 1990, Berger & Butler 2001). However, the risk of predation seldom is consistent temporally and spatially, and prey therefore may alter their behavior depending on their perceived predation risk. For example, an organism's perceived risk of predation may change with body size if predators are incapable of preying upon larger individuals (Ryer 1988, Orth & van Montfrans 2002). In Bahia de la Ascension, Mexico, solitary Caribbean spiny lobsters chose to inhabit smaller shelters scaled to their body size under conditions of high predation risk and low conspecific density, and chose to inhabit larger shelters that allowed aggregation under conditions of low predation risk and high conspecific density (Eggleston & Lipcius 1992). Shelter-dwelling organisms that are vulnerable to predators, such as lobsters, therefore must decide among different behaviors for predator avoidance based on perceived risk of predation, conspecific density, and habitat availability and quality.

We examined California spiny lobster *Panulirus interruptus* (Randall, 1840) predator avoidance behavior and size distribution under variable regimes of predation risk in southern California kelp forests. The California spiny lobster (Crustacea: Decapoda: Palinuridae) is an ecologically and economically important species in southern California and Baja California, Mexico. Predation by *P. interruptus* alters community structure within the intertidal zone (Robles et al. 1990) and may play a strong role in structuring communities in kelp forests as well (Tegner & Levin 1983, Halpern et al. 2006). California spiny lobster population size and mean size have decreased in response to heavy fishing pressure (Dayton et al. 1998). Thus, changes in predation pressure on California spiny lobsters may exacerbate the results of fishing and alter the intensities of top-down effects on subtidal and intertidal systems.

California spiny lobsters typically inhabit shelters during the day and emerge from shelters at dusk to forage (Allen 1916, Lindberg 1955). They may be found alone in shelter, but aggregations of 2 to 15 lobsters in shelters are common (Zimmer-Faust & Spanier 1987). Though the behavioral defenses of other panulirids (e.g. *Panulirus argus*) have been extensively studied, relatively little is known about the California spiny lobster's behavioral and morphological defenses to predators, though shelter use, gregarious behavior (aggregations), and large body size all may deter predators (Winget 1968, Zimmer-Faust et al. 1985, Zimmer-Faust & Spanier 1987, Spanier & Zimmer-Faust 1988). Daytime aggregations by panulirids may minimize the risk of predator-induced mortality, particularly for younger

individuals (Mitchell et al. 1969, Berrill 1975), by decreasing the per capita risk of predation (the dilution effect), enhancing group defense from predator attacks, and increasing vigilance against predators (Herrnkind et al. 2001). Antennae 'posturing' by *P. interruptus* also may be a form of defense against predators (Spanier & Zimmer-Faust 1988, C. L. Loflen pers. obs.). Additionally, *P. interruptus* is able to chemically detect conspecifics (Zimmer-Faust et al. 1985), which as for other panulirids, may quickly guide lobsters to suitable shelter, a process termed the 'guide effect' (Nevitt et al. 2000, Childress & Herrnkind 2001).

To examine how lobster behavior and size distribution varied with predation risk, we took advantage of large-scale differences in the abundance of top predators in the kelp forests of southern California. Our study sites within the La Jolla kelp forest were within the boundaries of the La Jolla Ecological Reserve (LJER), a small (2.16 km²) no-take marine protected area (MPA) established in 1973 at the northern end of the kelp forest. This MPA was established in response to diminishing populations of abalone and large predatory fishes such as California sheephead *Semicossyphus pulcher* and black sea bass *Stereolepis gigas*, both predators of spiny lobsters that are abundant in the MPA (Parnell et al. 2005). In contrast, the Point Loma (PL) kelp forest, 10 km to the south of the LJER, remains open to both commercial and recreational fishing and has vastly reduced densities of large predatory fishes (Dayton et al. 1998, C. L. Loflen pers. obs.). We conducted surveys and predation experiments in the LJER and in PL to determine whether differences in lobster predation risk exist between the 2 sites and whether these differences influence lobster antipredator behavior. Specifically, at each site we quantified (1) predator abundance, (2) relative lobster mortality, (3) lobster density and size distribution, (4) shelter characteristics, and (5) lobster shelter selection behavior.

MATERIALS AND METHODS

Study sites. Our surveys and experiments took place from June to September 2006 in the LJER and in PL (Fig. 1). The kelp forest at both sites is dominated by the surface canopy-forming giant kelp *Macrocystis pyrifera* and by 2 understory kelps, *Pterygophora californica* and *Laminaria farlowii*, growing at ca. 9 to 20 m depth (Stewart 1991, Dayton et al. 1992). The intertidal and shallow subtidal shorelines have extensive surfgrass *Phyllospadix torreyi* habitat that is used by juvenile and adult lobsters (Parker 1972, Serfling 1972, Engle 1979). Mean monthly water temperatures can range from 10 to 22°C, though temperatures below the thermocline rarely exceed 16°C (Stewart 1991). The
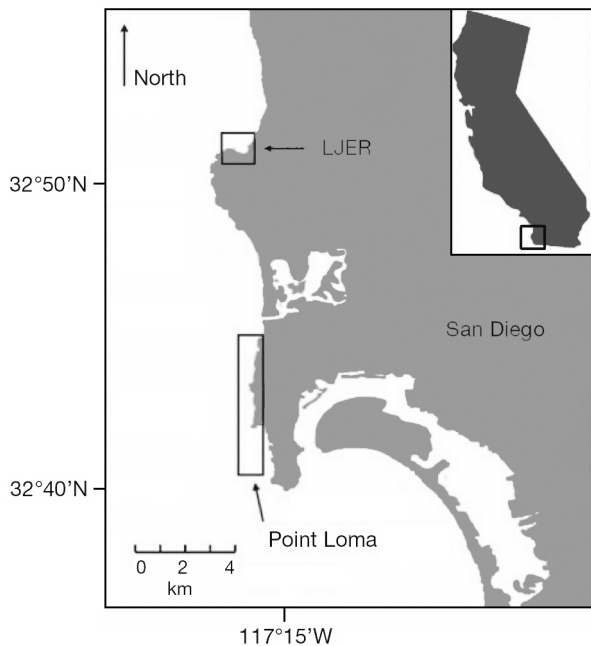
Fig. 1. The Point Loma kelp forest and the La Jolla Ecological Reserve (LJER) study sites in San Diego, CA, USA (32.69° N, 117.26° W)

substratum consists of gently sloping sandstone with scattered cobble to boulder-sized rocks of varying densities. Stacked cobble and boulders, ledges, and hollowed-out *M. pyrifera* holdfasts serve as lobster shelters. Commercial and recreational fishing for lobsters takes place in PL from October to March. Studies at both locations were conducted using SCUBA diving.

Relative lobster mortality. We used tethering to determine whether relative mortality rates of lobsters outside of shelter varied between the LJER and PL, and between juvenile (4 to 5 cm carapace length, CL) and adult (7 to 8 cm CL) lobsters. Tethering is frequently used to compare relative rates of crustacean mortality (e.g. crabs: Pile et al. 1996, Hovel & Lipcius 2001; lobsters: Mintz et al. 1994, Lipcius et al. 1998, Diaz et al. 2005) but does not measure absolute mortality rates because tethered prey cannot flee from predators. Lobsters were captured by hand ca. 24 h before experiments began and held in a recirculating aquarium. We tethered lobsters by cinching a noose composed of 36 kg braided fishing line around the carapace and then gluing the noose to the top of the carapace using cyanoacrylate glue. A 30 cm extension of the noose then was tied to a stake affixed to the substratum. We tethered 4 replicate lobsters within each of 21 haphazardly located plots in the LJER and PL. Lobsters in plots were tethered no less than 14 m apart and plots were never reused. As our goal was to assess relative predation risk between sites for lobsters outside of

shelter, all understory algae within a 1 m radius around tethered lobsters was cleared at the start of each trial. Each trial lasted 7 d and there were a total of 11 and 10 trials in the LJER and PL, respectively, for a total of 40 lobsters (n = 20 per size class) in the LJER and 44 (n = 22 per size class) in PL. Lobsters not consumed after 7 d were released at the point of capture. After 7 d we recorded the state of the lobster as alive (whole, active lobster remaining on the tether), eaten (fragment of the carapace remaining on the tether), missing (no lobster or fragment remaining on the tether), or molted (entire carapace remaining on the tether). Molted lobsters were excluded from the analysis. Previous work with California spiny lobsters indicated that they could only escape from a tether via molting and that there was no indication of tethering inducing molting or mortality within a 7 d tethering period (Mai & Hovel 2007). We tethered an additional 6 lobsters in control cages and found no mortality or escapes from tethers. Additionally, video analysis of tethered lobsters (see section below) revealed that large fish predators often remove lobsters entirely from tethers. We therefore assumed that missing lobsters were taken away by predators. We tested for differences in relative lobster mortality between the LJER and PL and between juvenile and adult lobsters using a *G*-test.

Video analysis. We tethered an additional 3 lobsters in the LJER and 5 lobsters in PL and used a digital video camera in a waterproof housing to identify lobster predators, evaluate length of time before a predator encounter, and to enumerate predator strikes on lobsters in each region to qualitatively assess if there was any treatment-specific bias between regions (Peterson & Black 1994).

Lobster, predator, and shelter surveys. We conducted surveys in the LJER and PL to quantify patterns of shelter density and lobster density, size distribution, and shelter use. We also conducted surveys for large predatory fishes in each location to estimate potential predator density, and thus the perceived predation risk for lobsters surveyed. Surveys at both locations were done in depths of 9 to 14 m. In PL, we counted lobsters and potential lobster shelters in 12 haphazardly chosen sites (20 × 20 m) located no less than 100 m apart (Mai & Hovel 2007). At each site, divers searched for shelters and lobsters by swimming 4 parallel 5 × 20 m transects, covering the entire 400 m². Divers recorded the number of lobsters per shelter and also searched for lobsters outside of shelter by turning over understory algae while conducting the transects. Lobster CL was measured to the nearest 0.5 cm with a ruler. Lobster shelters were characterized as (1) ledge (cracks in the reef forming permanent crevices or overhangs), (2) rock (spaces between rocks or between rocks and the substratum), or (3) holdfast (giant kelp holdfasts

hollowed out by grazing sea urchins). Lobsters commonly are found in all 3 of these shelter types in southern California (Mai & Hovel 2007). For each shelter, we recorded shelter dimensions by taking 3 haphazard measurements each for depth, opening height, and width. Empty shelters were measured and investigated for organisms that can competitively exclude lobsters (e.g. octopus). In the LJER, lobster and shelter surveys were identical to those conducted in PL except that, due to the smaller size of the kelp forest, we counted lobster and shelters in 13 haphazardly chosen 4 × 20 m sites located no less than 50 m apart.

To quantify the abundance of potential lobster predators in the LJER and PL, we counted the number of California sheephead *Semicossyphus pulcher*, black sea bass *Stereolepis gigas*, horn sharks *Heterodontus francisci*, kelp bass *Paralabrax clathratus*, cabezon *Scorpaenichthys marmoratus*, and ling cod *Ophiodon elongatus* observed within transects at the same sites used to survey lobsters and shelters. These abundant fishes represent the majority of large-bodied potential lobster predators in southern California (Winget 1968, Cowen 1986). Potential lobster predators not accounted for in these surveys included octopuses *Octopus* spp. and the California sea lion *Zalophus californianus*. Fishes <30 cm in length were not considered potential predators of juvenile and adult lobsters, based on video analysis of potential predator strikes (see 'Video analysis' above) and from previous tethering experiments (Mai & Hovel 2007). Surveys were made by swimming slowly along the bottom and counting the number of potential predators of each species within a 4 × 20 m transect and up to 4 m above the substratum (Parnell et al. 2005). While some large fishes may remain out of visual range of divers, and fish behavioral differences between MPA and non-MPA locations may make comparisons among locations conservative (Kulbicki 1998), survey by SCUBA diving is the most effective method for estimating large fish densities in southern California kelp forests (Davis & Anderson 1989).

To compare lobster and shelter characteristics between the 2 sites, we used a multivariate analysis of variance (MANOVA), followed by 2-tailed *t*-tests, to test for differences in mean lobster density, mean shelter density, and mean lobster CL between the LJER and PL. Data were log-transformed when necessary to meet test assumptions in these and all subsequent tests. Assumptions of normality were evaluated visually while those of homogeneity of variances were evaluated using the *F*-test. We further examined shelter characteristics by performing a Kolmogorov-Smirnov (K-S) test to detect differences in the distributions of available shelter volumes between sites. To determine whether solitary lobster shelter use varied

between the 2 sites, we began by testing whether mean shelter opening height differed between the 2 sites with a 2-tailed *t*-test and then tested whether solitary lobsters used shelters more closely scaled to their body size in the LJER than in PL (Eggleston et al. 1990). To do so, we used linear regression to test for correlations between lobster CL (dependent variable) and shelter aperture (opening) height (independent variable). We chose shelter aperture height as the independent variable, rather than shelter volume, width, or depth, because shelters with lower entrance height restrict access to large fishes, and Caribbean spiny lobsters that chose shelters with an aperture height scaled closely to body size received greater protection from fish predators than lobsters selecting taller shelters (Eggleston et al. 1990, Mintz et al. 1994). We tested for differences between the 2 locations by comparing the equality of the slopes between the 2 best-fit regression lines using a *t*-test (Zar 1999). The data for this analysis were limited to lobsters with the same range of CL between the 2 sites (i.e. 5.5 to 8.5 cm CL). Additionally, we used separate chi-square tests for independence to test for differences in (1) the proportion of solitary lobsters that were juveniles, (2) the proportion of aggregations (2 or more lobsters) containing at least one adult lobster, and (3) the number of lobsters found outside of shelter during the day between the LJER and PL. We also compared the distribution of aggregation sizes with the Poisson distribution utilizing a chi-square goodness-of-fit test to determine if lobster aggregations were significantly larger than those expected by chance (Zimmer-Faust et al. 1985, Zimmer-Faust & Spanier 1987). Lastly, we used separate chi-square tests for independence (one for each species) to test for differences in predator presence between the 2 sites. Yates correction was used when necessary to adjust analyses for low predator abundance.

RESULTS

Relative lobster mortality

Of all lobsters tethered, only one escaped via molting, and no lobsters tethered in control cages escaped from tethers, died, molted, or were eaten. Mortality from predation was significantly higher for juvenile and adult lobsters in the LJER than in PL, but there was no difference in mortality between juvenile and adult stages and no interactive effect of site and stage (*G*-test, Stage: df = 1, $G = 0.27$, p = 0.27; Site: df = 1, $G = 57.72$, p < 0.001; Site × Stage: df = 1, $G = 0.26$ p = 0.61; Fig. 2). In the LJER, 89.5 % of adult lobsters and 100 % of juvenile lobsters were eaten within 1 wk of tethering,
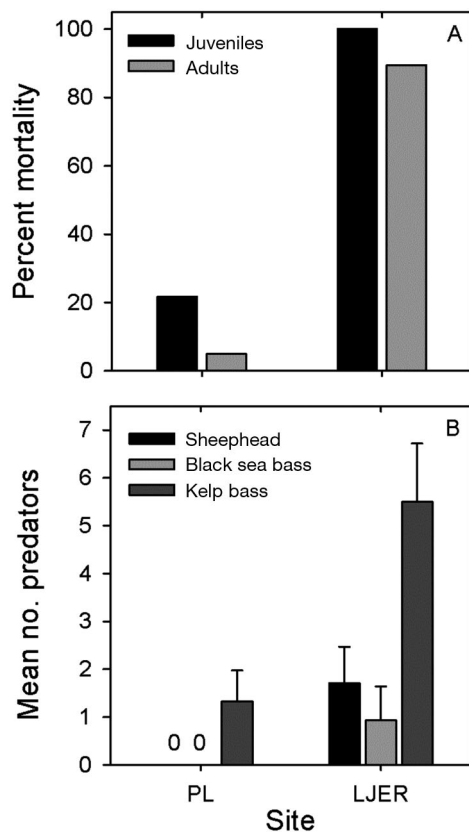
Fig. 2. (A) Relative percent mortality for juvenile and adult spiny lobsters *Panulirus interruptus* in tethering experiments conducted in the Point Loma (PL) kelp forest and the La Jolla Ecological Reserve (LJER). (B) Mean (+SE) number of potential predators per 20 m transect at the 2 sites

Table 1. *Panulirus interruptus.* Results of *t*-tests for differences in lobster characteristics, site characteristics, and lobster shelter use between the La Jolla Ecological Reserve and the Point Loma kelp forest

Factor	df	*t*	p
Mean lobster density	23	1.23	0.22
Mean lobster size	270	9.8	<0.01
Mean shelter density	23	3.1	<0.01
Mean shelter volume	284	1.96	0.05
Mean shelter height	284	0.08	0.93

Lobster and shelter characteristics

Over the course of our surveys, we counted and measured 151 shelters and 125 lobsters in the LJER, and 147 shelters and 153 lobsters in PL. Collectively, lobster density, shelter density, and CL differed between sites (MANOVA: df = 3, 21, F = 4.429; p < 0.05). Mean lobster density was 3-fold higher in the LJER than in PL, but the trend was weakened by high within-site variance in the LJER (Table 1, Fig. 3). We found strong evidence for greater mean lobster CL in the LJER than in PL (Table 1, Fig. 4). We compared mean lobster CL at each site to average size at reproductive maturity for California spiny lobsters (6.5 cm CL; Barsky 2001) and found that lobsters in the LJER were on average significantly larger than the size of reproductive maturity (df = 119, t = 5.9, p < 0.001), while average size of lobsters in PL was significantly smaller than the size of reproductive maturity (df = 151, t = 8.2, p < 0.001).

We found strong evidence for higher shelter density in the LJER than in PL (Table 1, Fig. 3) and marginally strong evidence that mean shelter volume was larger in the LJER than in PL (Table 1, Fig. 5), but little evi-
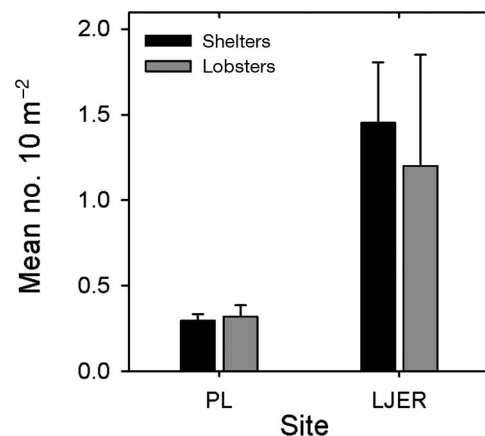
compared to 5% of adults eaten and 29.4% of juveniles eaten in PL. In the qualitative video analysis, California sheephead were the primary predator in the LJER, typically consuming lobsters within 1 h of tethering. In PL, no lobsters were consumed or attacked in a total of 450 min of video analysis.

Predator surveys

The abundance of potential predators was far higher in the LJER than in PL (Fig. 2). Divers observed potential predators on 100% of transects in the LJER, whereas only 58.3% of all PL transects contained potential predators (Yates-corrected chi-square, df = 1, χ^2 = 4.79, p = 0.029). Large numbers of California sheephead and black sea bass were present in the LJER but were entirely absent in our surveys in PL. Kelp bass were present at both sites, but their densities were 4-fold higher in the LJER than in PL (*t*-test: df = 1, 24, t = 3.38, p = 0.002; Fig. 2).

Fig. 3. *Panulirus interruptus.* Mean (+SE) California spiny lobster density and mean shelter density in the Point Loma kelp (PL) forest and the La Jolla Ecological Reserve (LJER)
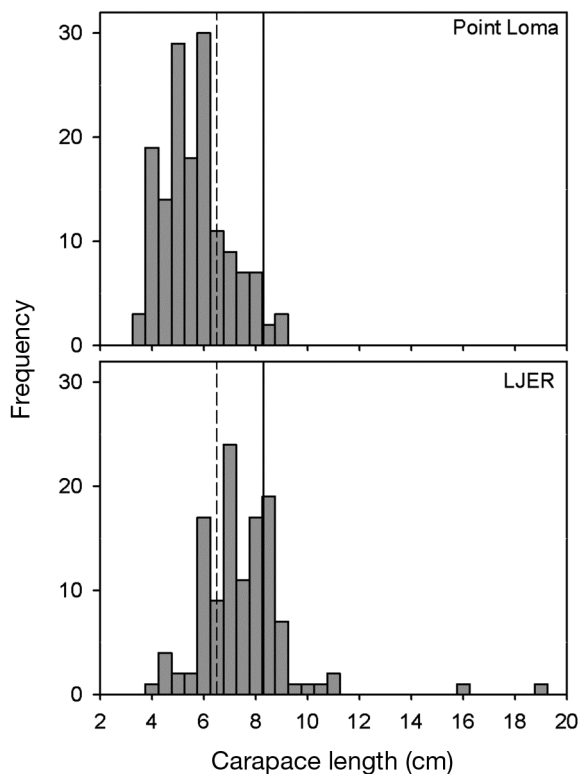
Fig. 4. *Panulirus interruptus.* Size-frequency distribution of spiny lobster carapace length (CL) for the Point Loma kelp forest and the La Jolla Ecological Reserve (LJER). Solid vertical line represents the minimum size of a lobster legally taken by the fishery (8.3 cm); dashed vertical line represents the minimum CL of reproductively active lobsters (6.5 cm)
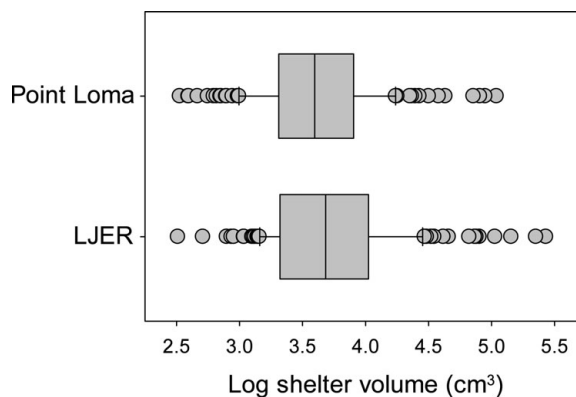

Fig. 5. Shelter-volume distribution for all available shelters surveyed in the Point Loma kelp forest and the La Jolla Ecological Reserve (LJER). Box limits: 25th/75th percentiles; whiskers: 10th/90th percentiles; middle box line: median; circles: outliers
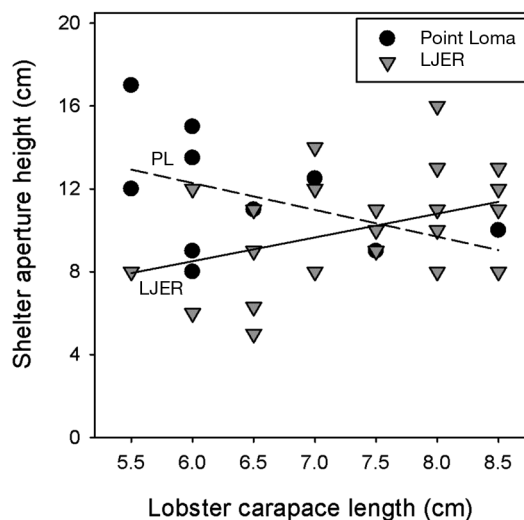

Fig. 6. *Panulirus interruptus.* Scatterplot of solitary spiny lobster carapace length versus shelter aperture height for the Point Loma (PL) kelp forest and the La Jolla Ecological Reserve (LJER). Dashed line for non-significant correlation in PL is shown to illustrate significantly different slopes of best fit lines for the 2 sites

dence for a difference in the distribution of shelter volumes available at each site (K-S Z statistic = 0.12, p = 0.24). There was also no evidence that mean shelter aperture height differed between sites (Table 1). The proportion of available shelters occupied by lobsters was relatively low at both the LJER and PL, with 27.1 and 39.1% of available shelters surveyed being occupied, respectively.

Lobster behavior

Though mean shelter height was nearly identical between the 2 sites, we found strong evidence that solitary lobsters use shelters more closely scaled to body size in the LJER. Shelter aperture height and lobster CL for solitary lobsters in the LJER were significantly correlated (df = 1, 21, F = 3.6, r^2 = 0.11, p = 0.07; Fig. 6), though much of the variation in shelter aperture height remained unexplained. In contrast, no correlation between shelter aperture height and lobster

CL for solitary lobsters existed in PL (df = 1, 8, F = 1.8, r^2 = 0.08, p = 0.22; Fig. 6). Slopes of the best-fit regression lines for shelter aperture height versus lobster CL differed between the 2 sites (df = 29, t = 18.4, p < 0.001). Aggregations were more common than expected by chance in the LJER (df = 4, χ^2 = 14.569, p < 0.01) but not in PL (df = 4, χ^2 = 6.677, p = 0.15; Fig. 7). All aggregations (2 or more lobsters) in the LJER contained at least 1 adult lobster, whereas in PL only 62% of aggregations contained at least 1 adult (Table 2).
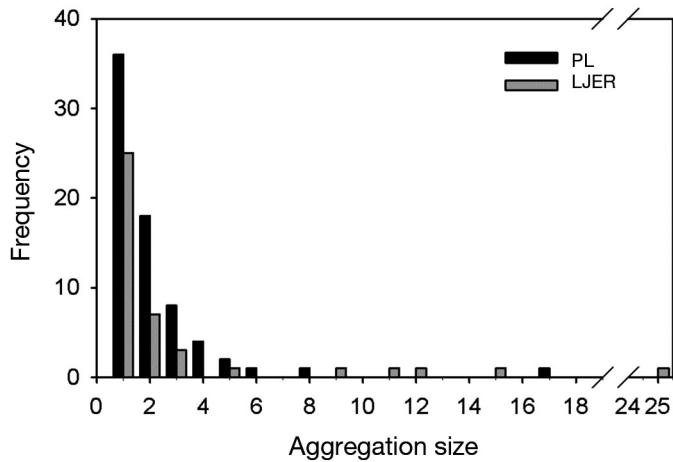
Fig. 7. *Panulirus interruptus.* Frequency of California spiny lobster aggregation sizes in the Point Loma (PL) kelp forest and the La Jolla Ecological Reserve (LJER)

There was also strong evidence for more lobsters outside of shelter in PL than in the LJER: In the LJER, no lobsters were witnessed outside of shelter, while in PL, 11.7% of lobsters surveyed were not in shelter, but instead were moving or stationary in unsheltered habitat during daylight hours (Table 2). Finally, the proportion of solitary lobsters classified as juveniles (<6.5 cm CL) was significantly lower in the LJER than in PL (Table 2).

DISCUSSION

Our primary finding in this study is that behavioral aspects of lobster shelter use varied between 2 kelp forest locations in southern California that differed substantially in predation risk. We found that the abundance of large predatory fishes and the relative mortality risk for lobsters were substantially higher in a small marine reserve (the LJER) than in nearby PL. Concomitantly, lobsters in the LJER selected shelters closely scaled to body size and more frequently inhabited shelters in aggregations than lobsters in PL. Lob-

sters in the LJER also were never observed venturing from shelter during the day, a behavior seen frequently during the day in PL.

An important caveat in our study is that we worked at only 2 sites, and therefore we cannot definitively ascribe patterns of lobster shelter use to mortality risk. Many factors that may influence shelter use likely differ among the 2 kelp forests in addition to predator abundance and risk of mortality outside of shelter, including lobster density, substratum rugosity, and the density of potential prey such as urchins (Nichols 2009). There also may have been aspects of potential lobster shelters that varied between sites that we did not quantify, as well as other features of the benthos, such as the density of understory algae, which may influence lobster mortality and behavior.

Despite covariation among a number of factors that differ between the LJER and PL, several lines of evidence suggest that strong differences in predator abundance and in relative mortality risk remain the most compelling reasons for differences in lobster shelter use behavior. First, altered patterns of shelter use form the basis of behavioral responses to predation risk in other lobster species, such as the Caribbean spiny lobster *Panulirus argus* (Eggleston & Lipcius 1992, Smith & Herrnkind 1992, Childress & Herrnkind 1997), the rock lobster *Jasus edwardsii* (Kelly et al. 1999), and the American lobster *Homarus americanus* (Spanier et al. 1998). For instance, when predation pressure was low in manipulative experiments, solitary *P. argus* chose large shelters suitable for future cohabitation (Eggleston & Lipcius 1992). However, when a predatory nurse shark was present, lobsters chose smaller, artificial shelters that were more scaled to their body size, as the relative mortality of juvenile lobsters was dependent upon the size of shelters in which they were tethered (see also Eggleston et al. 1990). Eggleston et al. (1997) found the same trend for increasing use of smaller, artificial shelters by solitary Caribbean spiny lobsters at sites with enhanced densities of predatory Nassau grouper in Sugar Cay Bay, Bahamas. Ours is the first study to test spiny lobster shelter scaling in response to mortality risk in naturally occurring shel-

Table 2. *Panulirus interruptus.* Results of chi-square tests on California spiny lobster shelter use behavior within the La Jolla Ecological Reserve (LJER) and the Point Loma kelp forest (PL)

Variable	LJER (%)	PL (%)	df	χ^2	p
Aggregations with: ≥ 1 adult[a]	100	62	1	8.3	0.004
Lobsters outside of shelter	0	11.7	1	15.7	<0.001
Solitary juvenile lobsters[b]	16.6	73.7	1	14.7	<0.001

[a]Proportion of lobster aggregations that contained ≥1 adult
[b]Proportion of all solitary lobsters classified as juveniles

ters, rather than artificial shelters. In our study, shelter height scaled with lobster body size where predation risk was high; in particular, smaller, vulnerable lobsters selected shelters with reduced aperture heights in the LJER as compared to lobsters in PL. Shelter aperture height may be the most important aspect of shelter size for lobsters; shelters with lower aperture height restricted predator access to Caribbean spiny lobsters in Bahia de la Ascension, Mexico (Eggleston et al. 1990), in Florida Bay (Mintz et al. 1994), and in Sugar Cay Bay (Eggleston et al. 1997). Differences in lobster shelter selection between the LJER and PL decreased as lobster body size increased, most likely because large lobsters have some size refuge from predation, particularly when occupying shelter.

A second reason to suspect that predation risk drives differences in lobster behavior between sites is that aspects of gregarious shelter dwelling, another antipredator behavior, differed between the LJER and PL. We found that the frequency of aggregations was greater than expected by chance in the LJER but not in PL, despite the higher density of potential shelters present in the LJER. Lobsters were not forced to form larger aggregations in the LJER than in PL, as shelter volumes were similar between the 2 sites, and many available shelters were unoccupied at both sites. Similarly, in large experimental arenas in Long Key, Florida, USA, lobsters were solitary or formed small groups when triggerfish predators were absent, but formed larger aggregations and limited their movements from shelter when triggerfish were present (Herrnkind et al. 2001). In Florida Bay, Caribbean spiny lobsters aggregated under large artificial shelters at sites with high predator abundance and high conspecifc density, and aggregations reduced proportional mortality of lobsters (Mintz et al. 1994). However, when predator abundance increased substantially and conspecific density decreased, lobster abundance within smaller, artificial shelters increased.

Third, we found lobsters outside of shelter during the day in PL, but not in the LJER. Lobsters and other shelter-dependent organisms may respond to reduced predation risk by reducing time spent in shelter (Herrnkind et al. 2001) and may gain an advantage over sheltered conspecifics via increased time spent foraging in productive habitats or an ability to move over larger distances. The presence of submerged vegetated habitat appears to influence whether California spiny lobsters emerge from shelter and which shelters they occupy during the day. For instance, lobsters outside of shelter during the day in PL invariably are found near or under understory algae (e.g. *Eisenia arborea* and *Pterygophora californica*) or within surfgrass *Phyllospadix* spp. beds, 2 habitats that afforded tethered lobsters protection from predators compared to unvegetated areas (Mai & Hovel 2007, Withy-Allen 2010). Moreover, for those lobsters that remained in shelter during the day in PL, abundance within rocky shelters at the landscape scale (i.e. 20×20 m areas) was positively correlated with the cover of canopy-forming understory kelp (Mai & Hovel 2007). Similarly, canopy-forming understory kelps also were abundant in the LJER and increased relative survival of lobsters compared to unvegetated areas; however, lobster shelter selection was influenced by the presence of the non-canopy forming alga *Plocamium pacificum*, which lobsters do not inhabit during the day, but which they use as foraging grounds at night to feed on small mollusks and crustaceans (Withy-Allen 2010).

We also found that juvenile lobsters exhibited strong differences in shelter-dwelling behavior between the 2 sites. Juvenile lobsters likely are vulnerable to a larger size-range of predators or at least may have a higher perceived risk of predation than larger lobsters. Relative mortality of tethered juveniles was higher than that of adults both in the LJER and at PL, though the difference was not statistically significant at either site (see also Withy-Allen 2010), and the relative mortality of juveniles in PL was much lower than LJER. Juveniles commonly occupied shelters alone in PL, but rarely did so in the LJER, and when this occurred in the LJER, they selected smaller shelters than did juveniles in PL. Moreover, aggregations consisting only of juveniles (as opposed to aggregations including at least 1 adult) were absent from the LJER but relatively common in PL. Though we cannot determine if this is a response to predation risk or to the fact that juvenile lobsters are more common at PL than in the LJER, juvenile Caribbean spiny lobsters experienced enhanced survival when sheltering in groups that included adult lobsters (Briones-Fourzan & Lozano-Alverez 2008). In contrast, Childress & Herrnkind (2001) found that juvenile Caribbean spiny lobsters benefited from gregarious shelter dwelling only via the guide effect (whereby searching lobsters locate shelters most quickly when they are occupied by conspecifics) rather than from enhanced rates of survival. However, modeling by Dolan & Butler (2006) predicted juvenile Caribbean spiny lobsters to benefit from enhanced survival via the guide effect only under conditions of low shelter density, longer shelter search period, and high predation risk.

Our results suggest that lobsters have made a major behavioral adjustment to reduced predation risk in PL. In contrast, present levels of predation risk for lobsters in the LJER may be similar to historical levels throughout southern California, particularly at times when large predatory fishes were still common in areas such as PL (Dayton et al. 1998). For example, at the turn of the 20th century, black sea bass and sheephead were

common in PL, and many reportedly had up to one dozen lobsters in their stomachs (Allen 1916). Sheephead are the dominant diurnal predator of California spiny lobsters and sea urchins, and their presence strongly deters lobster and urchin movement from shelter during the day (Allen 1916, Tegner & Levin 1983). Spiny lobsters may fill at least part of the role played by sheephead, which are now largely absent from PL, in top-down regulation of kelp forest communities (Tegner & Dayton 1981), particularly if daytime foraging by a subset of lobsters has led to increased lobster predation on herbivores such as the purple sea urchin *Strongylocentrotus purpuratus*. However, further research is necessary to determine how these behavioral shifts may alter benthic communities.

Though our study was too limited to suggest whether shelter use behavior is likely to differ between MPA and non-MPA sites in general, our results suggest that research on the effects of MPAs on benthic communities should consider how the establishment of MPAs may lead to changes in organism behavior and abundance. Higher-order predators, in particular, are often more abundant inside versus outside of MPAs (Cole et al. 1990, Babcock et al. 1999, Paddack & Estes 2000, Parnell et al. 2005), which can potentially induce indirect effects within these areas that should be studied further. Trait-mediated, indirect effects, including habitat selection, time spent outside of shelter, and prey choice by mesopredatory organisms such as lobsters, may have significant roles to play in how benthic communities respond to MPA establishment.

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